

How to map potential mesovoid shallow substratum (MSS) habitats? A case study in colluvial MSS

Rita P. Eusébio¹, Paulo E. Fonseca², Rui Rebelo¹,
Maria da Luz Mathias³, Ana Sofia P. S. Reboleira^{1,4}

1 Center for Ecology, Evolution and Environmental Changes (cE3c) & CHANGE – Global Change and Sustainability Institute, and Departamento de Biologia Animal, Faculdade de Ciências, Universidade de Lisboa, Lisbon, Portugal **2** Instituto Dom Luiz (IDL), Faculdade de Ciências, Universidade de Lisboa, Campo Grande, 1749–016, Lisbon, Portugal **3** CESAM and Departamento de Biologia Animal, Faculdade de Ciências, Universidade de Lisboa, Lisbon, Portugal **4** Natural History Museum of Denmark, University of Copenhagen, Universitetsparken 15, 2100 Copenhagen East, Denmark

Corresponding author: Ana Sofia P. S. Reboleira (asreboleira@fc.ul.pt)

Academic editor: Fabio Stoch | Received 14 October 2022 | Accepted 28 February 2023 | Published 21 April 2023

<https://zoobank.org/7CAFCCEC-462F-4737-AF92-822C3E2D351D>

Citation: Eusébio RP, Fonseca PE, Rebelo R, Mathias ML, Reboleira ASPS (2023) How to map potential mesovoid shallow substratum (MSS) habitats? A case study in colluvial MSS. Subterranean Biology 45: 141–156. <https://doi.org/10.3897/subtbiol.45.96332>

Abstract

Understanding habitat extension that limits species distribution is a crucial tool for management and conservation, in which habitat mapping plays a pivotal role. The mesovoid shallow substratum (MSS) is a type of shallow subterranean habitat with an important conservation value for invertebrate communities, functioning as climatic/reproductive refuge, biogeographic corridor and/or permanent habitat. Methodologies to map the mesovoid shallow substratum (MSS) are currently lacking. We propose a novel method for colluvial MSS habitat mapping, combining geographic information systems, geological maps, and geological knowledge on the habitat genesis. We tested and validated the efficiency of the method using the Arrábida karst area (Portugal) as a model. The method allowed the remote detection of MSS habitats suitable for invertebrate communities *ex situ* within the study area, and enabled the estimation of habitat extent. The faunal communities sampled in the selected location were dominated by arthropods, especially insects, showcasing the efficacy of this mapping method to detect suitable MSS habitats. The use of this method considerably reduces the *in situ* scouting area, providing a more efficient way of locating these habitats. The MSS is protected under EU legislation concerning floral communities and geological features, completely neglecting its faunal communities. This method also allows to estimate potential MSS habitat extension in several lithologies, facilitating the implementation of invertebrate prospecting, and the establishment of more effective conservation measures.

Keywords

Arrábida Natural Park, habitat mapping, scree slopes, shallow subterranean habitats, subterranean ecosystems, Portugal

Introduction

The Mesovoid Shallow Substratum (or Stratum) was described in French as the “*Milieu Souterrain Superficiel*” (MSS) by Juberthie et al. (1980) in the Pyrenees, as an extensive type of shallow subterranean habitat, “formed by a network of air-filled voids and open spaces in between rock fragments” (for recent review on terminology see Mammola et al. 2016). Like caves, the MSS is characterized by total darkness, stable temperatures, and high humidity levels (Culver and Pipan 2014; Mammola et al. 2016; Nitzu et al. 2018).

Colluvial MSS, one of the four recognized types of MSS (Mammola et al. 2016), is typically composed of homogeneous rock material (depending on the type of bedrock) in various and heterogeneous sizes. The colluvial material consists of unconsolidated free sediments that have been deposited on hillslopes by either rain-wash, slow continuous downslope creep, or a combination of both these processes (Juberthie et al. 1980; Jiménez-Valverde et al. 2015). This type of MSS, when exposed is referred to as a scree slope, but can also be covered by a layer of soil and vegetation (Culver and Pipan 2009).

The MSS can be inhabited by organisms with different adaptations to life in subterranean habitats, from surface ones living in the soil (edaphic), to species with some affinities to the subterranean habitats (troglophile), to animals fully adapted and dependant on the subterranean habitat to survive (troglobiont) (Ortuño et al. 2013; Culver and Pipan 2014; Nitzu et al. 2014). It has been studied in several countries, mainly for its faunal communities, which are dominated by insects and other arthropods (Pipan et al. 2010; Rendoš et al. 2012; Ortuño et al. 2013; Nitzu et al. 2014; Jiménez-Valverde et al. 2015; Eusébio et al. 2021).

This habitat is an ecotone between surface and deeper subterranean habitats (Gers 1998), and can serve three very distinct, but equally important functions: 1) climatic/reproductive refuge for surface species, as in this habitat temperature variations along the year are much less extreme than at surface (Nitzu et al. 2011, 2014, 2018; Mammola et al. 2016); 2) biogeographic corridor to deeper ecosystems, as in many cases the MSS is connected to caves by a system of fissures, especially in karstic landscapes (Ortuño et al. 2013; Jiménez-Valverde et al. 2015); 3) permanent habitat for some species (Culver and Pipan 2009; Pipan et al. 2010; Eusébio et al. 2021).

Habitat mapping is a critical step for the management and conservation of habitats and their faunal communities (McDermid et al. 2005), as it allows an estimation of species distribution and richness patterns (Lecours et al. 2015), leading to the development of better monitoring protocols (Cogan et al. 2009; Lecours et al. 2015). Regarding subterranean habitats, improving habitat mapping methods will aid answering two

of the fundamental research questions on subterranean biology: “What is the species richness pattern of subterranean organisms globally?” and “What would be the best monitoring protocols to quantify long-term changes in the distribution and abundance of subterranean invertebrates?” (Mammola et al. 2020).

Subterranean habitats, “the most widespread non-marine environments on Earth” (Mammola et al. 2019), are particularly difficult to map due to their challenging access for humans (Mammola et al. 2019; Tanalgo et al. 2022). Caves have been mapped throughout the world since the beginning of speleological studies (Martel 1894), evolving into digital mapping (Trimmis 2018; Jones 2022; Kampolis et al. 2022), which include robots (Chang et al. 2022; Tabib et al. 2022) and remote sensing from space (Sharma and Srivastava 2022), using terrestrial lava tubes as models (Bell Jr. et al. 2022). On the other hand, the network of spaces and voids that composes the majority of subterranean habitats, which is inaccessible to humans, has never been mapped (Mammola et al. 2019).

This inaccessible underground network is the habitat that most subterranean species occupy, placing them “among the least documented fauna on our planet” (Mammola et al. 2019). Despite the different MSS types being properly described (Mammola et al. 2016), the worldwide extent of this habitat is currently unknown, with no available mapping methods proposed so far. Currently, its prospection relies solely on *in situ* visual verifications.

We propose a methodology to locate and estimate the areas of colluvial MSS habitats, using a combination of geographic information systems, geological maps, and geological knowledge on the genesis of this habitat. The Arrábida massif in Portugal was selected as the study area to develop, test, and validate the mapping method. The work conducted was divided into six steps: 1) defining a geological area to map, 2) defining main geological criteria for habitat genesis, 3) selecting potential locations using satellite imagery, 4) combining the potential sites with geological maps, in order to apply the criteria, 5) performing an *in situ* verification of the sites that met all the criteria, 6) assessing biodiversity in order to verify if the habitats selected by the method are suitable for typical MSS invertebrate communities.

Materials and methods

Literature review

Data on mapping methodology of shallow subterranean habitats was obtained from the available literature using: i) Elsevier Scopus with the following search topics “mesovoid AND shallow AND substratum” or “shallow AND subterranean AND habitats” or “milieu AND souterrain AND superficiel”; ii) Clarivate Web of Science with the same topics as i). Information harvested contains study location, MSS type, rock type, how the habitat was found, its extent, mapping method used, faunal taxonomic information, and type of results obtained in the study (Diversity, Taxonomy, Ecology).

Study area

The Arrábida karst massif (Portugal) was selected for the development of the habitat mapping method, due to its location in an area rich in invertebrate subterranean fauna (Reboleira et al. 2011), and the availability of geological maps and satellite images of the area.

The Arrábida chain is located in the southern edge of the Setúbal peninsula (Fonseca et al. 2014; Ramalho 2015), and is included in the homonymous Natural Park, created in 1976. The chain is particularly rich and diverse from a geological point of view (Parque Natural da Arrábida 2000), being comprised of a small group of mountains, oriented E-W and extending for 35 km, with the major accidents (thrusts and faults) verging to the South (Presas 2012; Fonseca et al. 2014), and a maximum altitude of around 500 m (Fonseca et al. 2015).

It is defined as a hard (high) relief, i.e., reliefs that stand out in height in comparison to the average altitudes of a region. This kind of hard reliefs are formed by the interaction of both erosive and tectonic processes (Fonseca et al. 2014). The erosive process occurs when there is a strong lithological contrast (Fonseca et al. 2014), i.e., when a relief has two different types of rock in contact with each other, one with a harder lithology (for example, crystalline limestones) and one with a softer lithology (for example, claystone or marlstone). In this case, there is a rapid erosion of the softer type of rock, leaving the harder one topographically exposed. This exposed hard rock will then erode slowly, first into boulders, and then into smaller and smaller rock fragments as they move down the slopes forming alluvial and colluvial fans. When rocky fragments reach the bottom of these slopes (and sometimes accumulate in deep structures) colluvial MSS is formed (Fonseca et al. 2015). The tectonic process consists of a compressive regime that resulted in the formation of faults and folds that sometimes duplicate by imbrication of the entire sequence. In the case of the Arrábida chain, these alternations oriented along the coast form cornices and cliffs, at the base of which the eroded sediments are deposited with little or no consolidation, forming colluvial MSS (Fonseca et al. 2014).

The Arrábida chain has a typical Mediterranean climate, characterized by two extreme seasons (a warm and dry summer, with prolonged drought periods, and a cold humid winter), and two mild seasons (spring and autumn) (ICNF 2015; Almeida et al. 2017). The fact that this chain faces the Atlantic Ocean leads to high air humidity levels (ICNF 2015). Its vegetation consists of a typical Mediterranean scrub, with *Ulex densus* and *Genista tournefortii* gorses, *Cistus albidus*, *C. ladanifer* and *C. monspeliensis* rockroses, *Quercus coccifera* and *Rhamnus alaternus* evergreen shrubs, and *Juniperus phoenicea* juniper (Parque Natural da Arrábida 2000).

Habitat mapping method

The first step in defining the mapping method for colluvial MSS habitats, of the scree slope type, was to define five main criteria for the selection of a location where this habitat might occur, taking into consideration all the conditions necessary for the geological formation of colluvial MSS (Table 1).

The second step was to select locations that seemed to possess “colluvial MSS properties”, i.e., locations where slopes filled with rocky fragments could be detected visually, using Google Earth software.

The third step was to rasterize the geological map of the area, in this case section 38-B Setúbal, Portugal (Industry and Energy Ministry, Geology and Mining Institute) in QGIS 3.14.16 software (QGIS Development Team 2020), and select the following lithological features from the Jurassic and Cretaceous periods: limestone, conglomerate and dolomite. These three formation types were chosen according to the general lithology of the study area, and within the parameters of Criteria 4 (Table 1).

The fourth step was to overlap the coordinates of the selected potential colluvial MSS locations with the rasterized map in QGIS 3.14.16 software, using a mapping system that provides contour lines to better identify erosion run-off zones. Each location was tested on the resulting map for the fulfilment of all five criteria established for potential colluvial MSS habitat identification (Table 1).

The fifth step was to conduct an *in situ* verification for the locations which met all the five criteria. These locations were characterized for facing direction (registered *in situ*) and estimated area (calculated using Google Earth software) (Suppl. material 1).

The total estimated colluvial MSS area within the Arrábida Natural Park was calculated based on the individual estimated area of each scree slope.

Maps were produced in QGIS 3.14.16 software. An open access “World Topographic Map” layer (Esri 1995), which allows the identification of the erosion run-off zones at a 96 dpi resolution, was used in the details of Fig. 3 to provide contour lines.

Preliminary biodiversity assessment

A preliminary biodiversity assessment was performed following previous methodologies of measuring biodiversity in MSS habitats (López and Oromí 2010; Eusébio et al. 2021), installing five modified pitfall traps (Fig. 1: Location 15) at a depth of 50 – 60 cm during two months (February and March of 2022) in one of the sites detected as MSS habitats by this method. The collected specimens were identified to order level, using a Leica S6E stereomicroscope, were stored in 96% alcohol and deposited at the Faculty of Sciences and the National Museum of Natural History and Science, University of Lisbon, Portugal.

Results

Literature review

Methodologies to detect and map MSS habitat were not found in any of the papers surveyed, neither methodologies to estimate habitat extent (Suppl. material 2).

MSS habitats have been studied for diversity, taxonomy, and ecology of invertebrate fauna in 15 countries, where around 65% focus on colluvial MSS, and around 43% do not inform the reader about the lithology of the study area, being the dominant lithology (when mentioned) karst areas (around 39%) (Suppl. material 2).

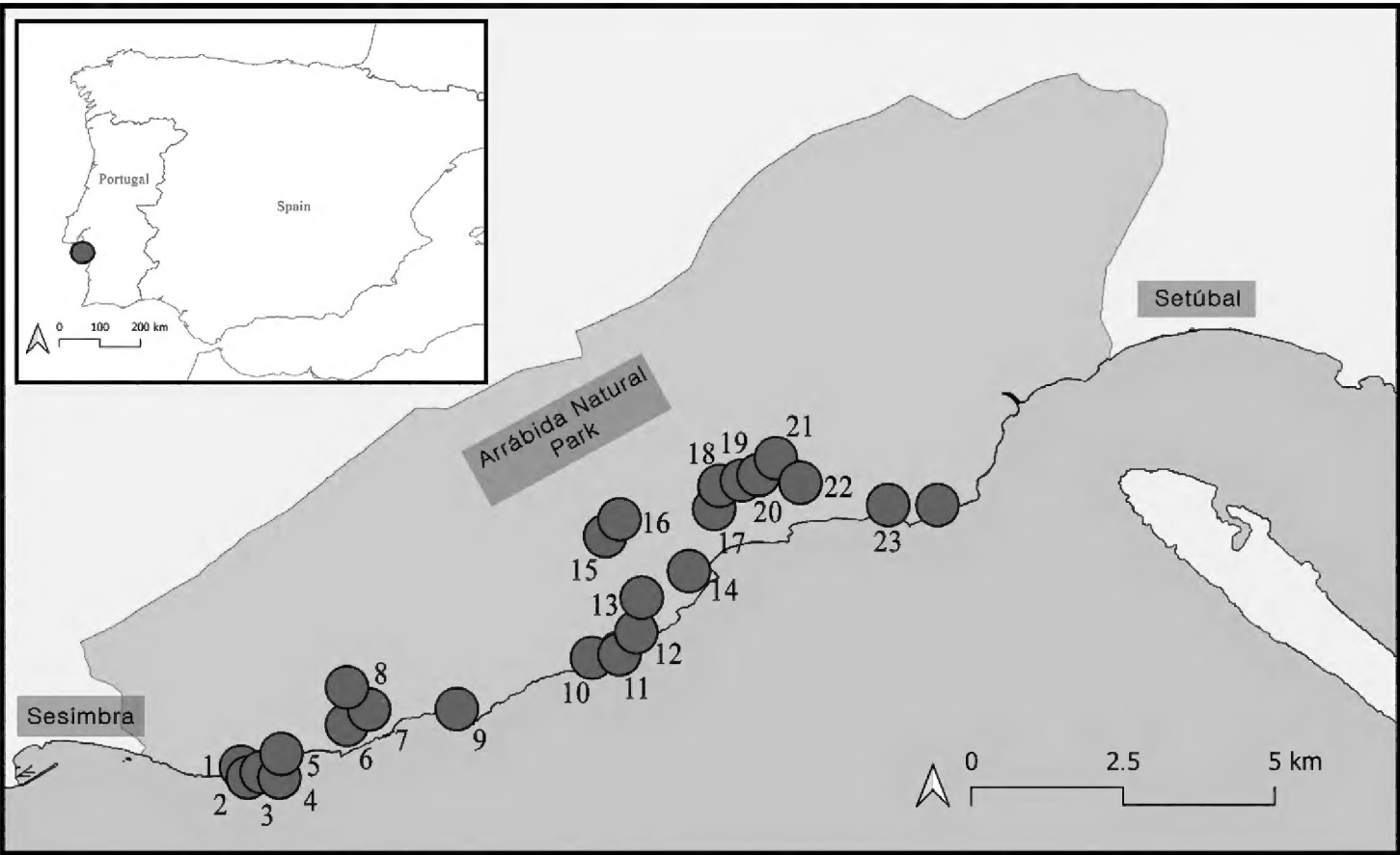


Figure 1. Potential colluvial MSS locations within the Arrábida Natural Park area, located between Sesimbra and Setúbal municipalities, Portugal.

Table 1. Criteria for identifying potential colluvial MSS habitats.

Criteria	Description	Justification
1	Reliefs present in the terrain	Reliefs consist of an exposed rock matrix that is elevated above ground level by either tectonic and/or erosive processes. This exposed matrix suffers subsequent erosion forming MSS habitats.
2	Strong lithological contrast in the relief	A strong lithological contrast means that there is a rapid erosion of a softer type of rock leaving adjacent harder rock exposed, leading to its later slow erosion into rock fragments and to the formation of scree slopes.
3	Erosion run-off zones	Considering that the parent rock is part of a relief, and that its erosion forms scree slopes, colluvial habitats form in steep slopes, below the exposed parent rock in the erosion run-off zone.
4	Adequate lithology	The type of rock selected needs to erode into fragments that can produce colluvial deposits. Example: limestones, conglomerates and marls (in karst areas), basalt (resultant of the erosion of volcanic cones).
5	Natural formation	The habitat needs to be formed by natural causes, and not by anthropogenic activities such as road construction and explosions associated with quarries, which form structures similar to colluvial MSS that are quite shallow or not connected with deep subterranean habitats.

Habitat mapping method

Potential colluvial MSS was initially indicated in 24 locations (Fig. 1). After applying the five criteria established for potential colluvial MSS habitat identification, 11 locations were considered eligible for an *in situ* verification (Suppl. material 3), of which eight were effectively confirmed to consist of scree slopes in the field (Figs 2, 3). The remaining three locations that fulfilled all criteria were observed in the field as completely covered by vegetation, and not as bare scree slopes.

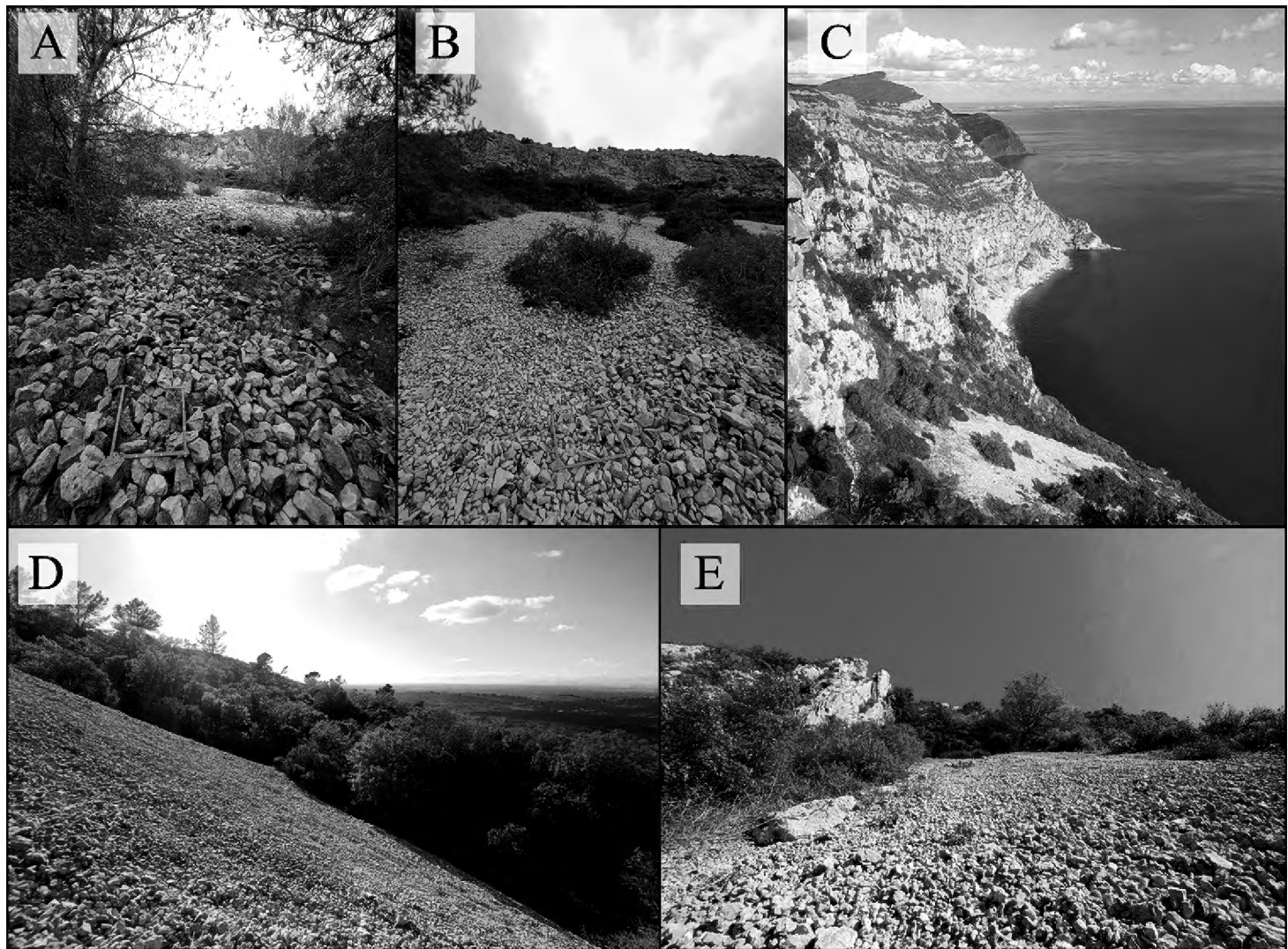


Figure 2. Locations that met all the five criteria established for potential colluvial MSS habitat identification. Locations: **A** 1 **B** 2 **C** 5 **D** 15 **E** 16.

Justification for locations meeting the defined criteria

Locations 1 through 4 are all within the erosion run-off zone right under 200 m a.s.l. (Fig. 3, Table 1: Criteria 1, 3). Location 5 is located in the erosion run-off zone at an elevation of 280 m (Fig. 3, Table 1: Criteria 1, 3). Locations 1 through 3 consist of dolomitic rocky fragments, while locations 4 and 5 are crystalline limestone (Fig. 3, Table 1: Criteria 2, 4). All factors point to a natural formation of these scree slopes (Fig. 3, Table 1: Criteria 5) as they are situated in low human intervention areas, and are quite exposed facing south and southeast (Suppl. material 1) which in this case means that they face the sea being, therefore, very prone to erosion by strong winds and rain.

Locations 15 and 16 are also within the erosion run-off zone right under 300 m a.s.l., on a limestone area (Fig. 3, Table 1: Criteria 1–4). Again, these scree slopes are very likely formed by natural processes as there is a parent rock exposed to the elements which faces northwest (Suppl. material 1), in a pristine area (Table 1: Criteria 5).

Location 21 is situated within the erosion run-off zone at 240 m a.s.l., in a limestone area (Fig. 3, Table 1: Criteria 1–4). This scree slope is likely formed by natural processes as there is a parent rock exposed to the elements (Table 1: Criteria 5), which faces northeast (Suppl. material 1).

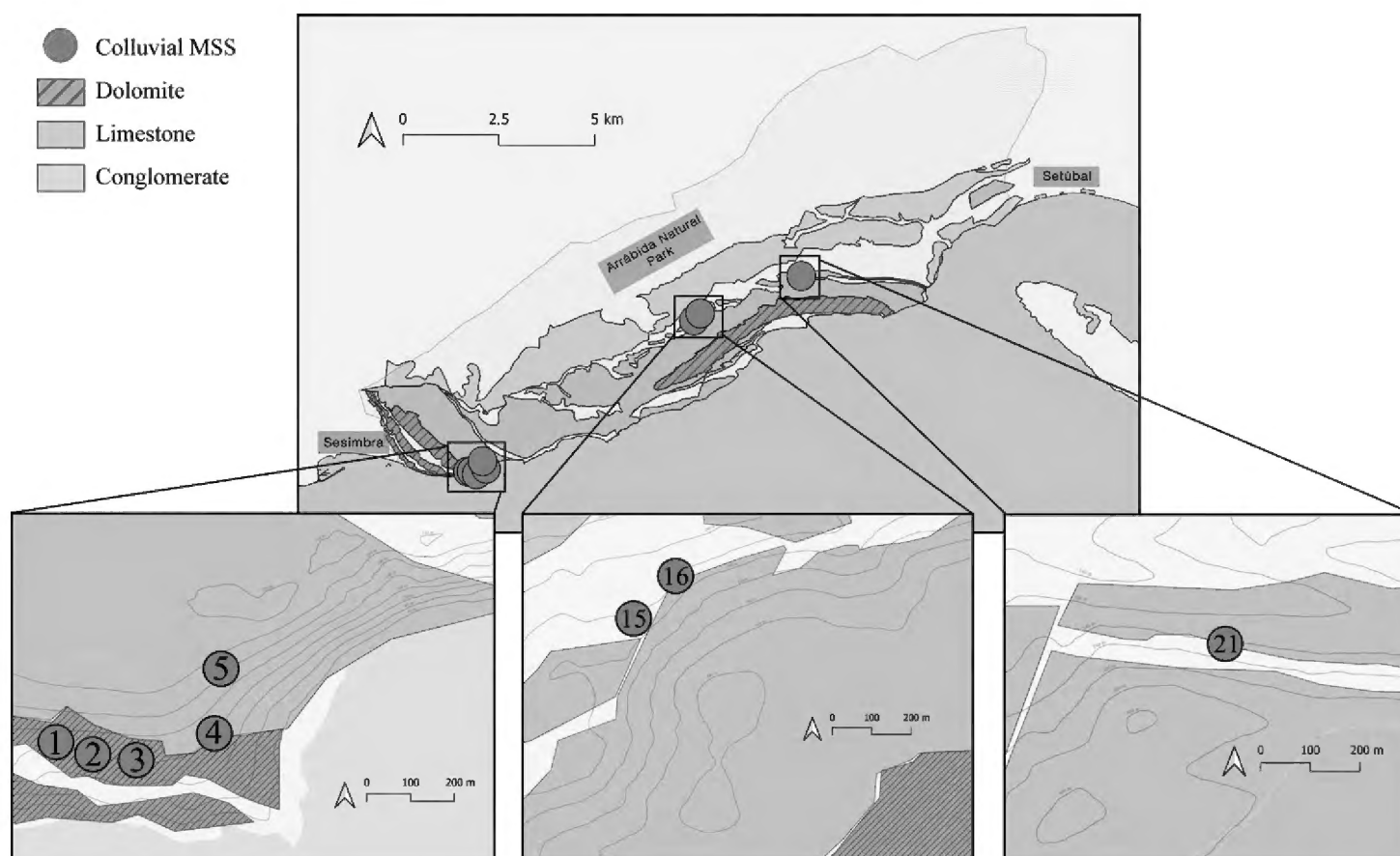


Figure 3. Map of the colluvial MSS locations confirmed *in situ*. Map of the Arrábida Natural Park, with the selected lithological feature layers (dolomite, limestone, and conglomerate), contour lines (in the three details), and colluvial MSS locations obtained with the proposed mapping method (numbered) confirmed *in situ*.

Estimated habitat area

The estimated areas for each of the scree slopes (Suppl. material 1) resulted in a total of approximately 30,500 m². This represents the total estimated surface area of colluvial MSS within the Arrábida Natural Park.

Habitat suitability for invertebrate fauna

A total of 551 invertebrate specimens were collected over the two winter months. About 98% of this community was represented by arthropods, with the remaining fauna being composed by molluscs (Suppl. materials 4, 5A). Over half of the arthropod specimens were insects, followed by Collembola (Suppl. materials 4, 5B). Within insects, Diptera's dominance was followed by Coleoptera and Hymenoptera (Suppl. materials 4, 5C). Among all taxa, a pseudoscorpion and a beetle presented troglomorphy, such as reduced eyes and depigmentation (Suppl. material 4), but the lack of male specimens precluded the determination to species level.

Discussion

This new habitat mapping method, combining geographic information systems with geological maps and information on MSS genesis, allows tracking and mapping

colluvial MSS habitats, improving the current habitat location technique, which is based on *in situ* verification.

This method also allows for the estimation of habitat distribution, and when applied to faunal studies allows the estimation of species distribution areas. This knowledge will in turn contribute to improve the establishment of protection and conservation measures for this habitat and its faunal communities.

The application of this method requires: 1) deciding whether the formation of the scree slope is natural or anthropogenic, as this criteria can be biased; 2) selecting appropriate rock types within the lithology of the study site, as long as they allow the formation of scree slopes (this includes non-karst areas) and 3) taking into account vegetation coverage of the area, which can mask scree slopes in the *in situ* verification stage (Rendoš et al. 2014; Rudy et al. 2018; Jakšová et al. 2019). One method to overcome this last complication is to add an updated vegetation layer to the mapping step, when available, in order to better predict these events. Other approaches can involve long term surveys, as vegetation coverage varies over time, especially in areas prone to wildfires (Bastos et al. 2011).

The initial scan of the study area using satellite imagery resulted in 24 locations for potential MSS habitats. With the use of geographic information systems and geological maps this number was reduced to eleven. After the visual *in situ* verification, eight locations were confirmed as the intended habitat, i.e., bare scree slopes. Our method has, therefore, proven to be effective in locating potential colluvial MSS habitats with around 75% accuracy after the *in situ* verification, and also considerably reducing the scouting area in the field.

Our results suggest that the sole use of GIS software to locate MSS habitats is less effective than our mapping method. This can be attributed to the lack of satellite image updating on certain areas of the country, especially natural areas, where vegetation grows fast, drastically changing the landscape in a short time (Clemente et al. 1996; Meira-Neto et al. 2011). The discrepancy between the locations meeting all the criteria, and the ones detected in the field can be explained by vegetation cover. Therefore, the “missing” locations are in fact colluvial MSS habitats covered by the thick vegetation found all over the area of the natural park, mainly *Quercus coccifera* shrubs (Parque Natural da Arrábida 2000).

The *in situ* verification for the presence of colluvial MSS in these locations was prevented due to the extremely dense vegetation in the field, which would require cutting down natural vegetation patches. MSS covered with soil and vegetation is common in the margins of bare scree slopes, which are gradually covered by mature soils, leading to more extensive plant coverage over time (Mammola et al. 2016; Giupponi et al. 2023). Therefore, our method also has the potential to detect “hidden” MSS areas, which are covered by soil and vegetation, continuous to the detected bare scree slopes.

In fact, the lithology of the area, previous observations, especially historical events related to wildfires (Clemente et al. 1996; Cruz and Viegas 1997), and knowledge of the natural park landscape (Parque Natural da Arrábida 2000) indicate the presence of MSS covered by soil and vegetation in those “missing” locations.

The mapping method also proved to be efficient in locating habitats suitable for invertebrate fauna. Scree slope habitats can host both surface and subterranean-adapted species (Pipan et al. 2010; Nitzu et al. 2011, 2014; Jiménez-Valverde et al. 2015). The communities found in the sampled location have a similar composition to communities typically found in the MSS in other European countries, i.e., the absolute dominance of arthropods, more specifically insects (Rendoš et al. 2012; Ortuño et al. 2013; Jiménez-Valverde et al. 2015; Eusébio et al. 2021), and few troglobiont species (Pipan et al. 2010; Jiménez-Valverde et al. 2015). However, we found an unusual pattern, the clear dominance in number of individuals of Diptera over Collembola. This can be linked with the lower altitude of our study (300 m a.s.l.), in contrast with the high mountain location of the previous studies (Rendoš et al. 2012; Jiménez-Valverde et al. 2015), as the abundance of several Diptera are known to be affected by elevational gradients and other climatic variables (Hodkinson 2004; Rhoner et al. 2015), but also by the lack of soil and vegetation coverage of bare scree slopes, that may facilitate the colonization of this habitat by flying insects.

This method allows a habitat extent estimation, which in the case of the colluvial MSS within the Arrábida Natural Park is approximately 30,500 m². This value corresponds to the surface area of habitat. However, like in other habitats, such as coral reefs (Dustan et al. 2013), the real extension of the MSS habitat is higher than its surface area, due to its three-dimensionality. Future studies to quantify the total MSS 3D area and volume will have to consider habitat depth and slope, rock fragment size, and rock occupied volume versus air filled spaces. It is also important to consider the area of the habitat that is covered by vegetation.

In Portugal, MSS habitats are protected by EU legislation in the Habitat Directive as “Western Mediterranean and thermophilic deposits”, in the “Limestone scree slopes (8130pt1)” subcategory, regarding plant communities and geological features (ICNB 2000). However, this protection completely disregards faunal communities, and, in a recent study, the Portuguese MSS was considered a habitat with high conservation value for invertebrate communities (Eusébio et al. 2021).

The use of this mapping method might facilitate the detection of MSS, which can later be studied and contribute to overcome the main shortfalls of subterranean biodiversity (Mammola et al. 2019) in shallow subterranean habitats. It will enable the increase of knowledge about habitat distribution (Racovitza shortfall), which will facilitate new faunal community studies (Mammola et al. 2019).

This new mapping method has the potential to be used worldwide, paying special attention to integrate topography, geomorphology, lithology and tectonic structures of the studied location, improving work efficiency for studies that deal with colluvial MSS, a more and more important habitat in the context of global changes as a climatic/reproductive refuge (Eusébio et al. 2021).

The possibility to survey the area of shallow subterranean habitats worldwide will help define conservation perimeters, and estimate the extent of occurrence (EOO) and area of occupancy (AOO) according to the IUCN Red List criteria (IUCN 2021) for species that inhabit shallow subterranean habitats. Moreover, our method allows for the estimation of the extension of this type of habitat around the world, which will certainly contribute to establish more effective conservation measures for land-use at surface and for faunal conservation.

Acknowledgements

This work was supported by the Portuguese National Funds through “Fundação para a Ciência e a Tecnologia” (FCT) within the cE3c Unit funding UIDB/00329/2020, CESAM (UIDP/50017/2020, UIDB/50017/2020, LA/P/0094/2020), PhD grant (2021.04868.BD), and by the VILLUM FONDEN (research grant 15471). All specimens were collected under the Instituto de Conservação da Natureza e das Florestas (ICNF). We are also grateful to the Arrábida Natural Park (PNA) for kindly providing accommodation, and to the park rangers for logistic support during fieldwork.

References

- Almeida L, Simões O, Melo R (2017) Análise e avaliação do potencial turístico dos territórios: o caso do parque natural da arrábida. *Exedra: Revista Científica* 1: 93–114.
- Bastos A, Gouveia CM, DaCamara CC, Trigo RM (2011) Modelling post-fire vegetation recovery in Portugal. *Biogeosciences* 8: 3593–3607. <https://doi.org/10.5194/bg-8-3593-2011>
- Bell Jr E, Schmerr N, Young K, Esmaeili S, Garry WB, Jazayeri S, Kruse S, Richardson J, Whelley P (2022) Field mapping and modeling of terrestrial lava tube magnetic anomalies as an analog for lunar lava tube exploration and prospecting. *Journal of Geophysical Research: Planets* 127: e2021JE007140. <https://doi.org/10.1029/2021JE007140>
- Chang Y, Ebadi K, Denniston CE, Ginting MF, Rosinol A, Reinke A, Palieri M, Shi J, Chatterjee A, Morrell B, Agha-Mohammadi A-A, Carlone L (2022) LAMP 2.0: A robust multi-robot SLAM system for operation in challenging large-scale underground environments. *IEEE Robotics and Automation Letters* 7: 9175–9182. <https://doi.org/10.1109/LRA.2022.3191204>
- Clemente AS, Rego FC, Correia AO (1996) Demographic patterns and productivity of post-fire regeneration in Portuguese Mediterranean maquis. *International Journal of Wildland Fire* 6(1): 5–12. <https://doi.org/10.1071/WF9960005>
- Cogan CB, Todd BJ, Lawton P, Noji TT (2009) The role of marine habitat mapping in ecosystem-based management. *ICES Journal of Marine Science* 66: 2033–2042. <https://doi.org/10.1093/icesjms/fsp214>
- Cruz MG, Viegas DX (1997) 1991 Arrábida Wildfire: analysis of critical fire weather conditions. *Silva Lusitana (Portugal)* 5(2): 209–223.
- Culver DC, Pipan T (2009) Superficial subterranean habitats – gateway to the subterranean realm? *Cave and Karst Science* 35: 9.
- Culver DC, Pipan T (2014) *Shallow subterranean habitats: ecology, evolution and conservation*. Oxford University Press, 266 pp. <https://doi.org/10.1093/acprof:oso/9780199646173.001.0001>
- Dustan P, Doherty O, Pardede S (2013) Digital reef rugosity estimates coral reef habitat complexity. *PLoS ONE* 8: e57386. <https://doi.org/10.1371/journal.pone.0057386>
- Esri (1995) World topographic map, Version 10.91. https://server.arcgisonline.com/arcgis/rest/services/World_Topo_Map/MapServer
- Eusébio RP, Enghoff H, Solodovnikov A, Michelsen A, Barranco P, Salgado JM, Sendra A, Reboleira ASPS (2021) Temporal and spatial dynamics of arthropod groups in terrestrial

- subsurface habitats in central Portugal. *Zoology* 147: 125931. <https://doi.org/10.1016/j.zool.2021.125931>
- Fonseca AF, Zêzere JL, Neves M (2014) Geomorphology of the Arrábida Chain (Portugal). *Journal of Maps* 10: 103–108. <https://doi.org/10.1080/17445647.2013.859637>
- Fonseca AF, Zêzere JL, Neves M (2015) Contribuição para o conhecimento da geomorfologia da cadeia da Arrábida (Portugal): Cartografia geomorfológica e geometria. *Revista Brasileira de Geomorfologia* 16: 137–163. <https://doi.org/10.20502/rbg.v16i1.533>
- Gers C (1998) Diversity of energy fluxes and interactions between arthropod communities: from soil to cave. *Acta Oecologica* 19: 205–213. [https://doi.org/10.1016/S1146-609X\(98\)80025-8](https://doi.org/10.1016/S1146-609X(98)80025-8)
- Giupponi L, Leoni V, Pedrali D, Zuccolo M, Cislighi A (2022) Plant cover is related to vegetation and soil features in limestone screes colonization: A case study in the Italian Alps. *Plant and Soil* 483: 495–513. <https://doi.org/10.1007/s11104-022-05760-3>
- Hodkinson ID (2005) Terrestrial insects along elevation gradients: species and community responses to altitude. *Biological Reviews* 80(3): 489–513. <https://doi.org/10.1017/S1464793105006767>
- ICNB (2000) Plano sectorial da Rede Natura 2000: Habitats naturais (8130). <https://www.icnf.pt/biodiversidade/natura2000/planosetorial>
- ICNF (2015) Parque Natural da Arrábida. <https://icnf.pt/conservacao/parques/parquenaturaldaarrabida>
- IUCN (2021) The IUCN Red List of threatened species. <https://www.iucnredlist.org/en>
- Jakšová P, Luptáček P, Miklišová D (2019) Distribution of Oribatida (Acari) along a depth gradient in forested scree slopes. *Subterranean Biology* 31: 29–48. <https://doi.org/10.3897/subtbiol.31.36241>
- Jiménez-Valverde A, Gilgado JD, Sendra A, Pérez-Suárez G, Herrero-Borgoñón JJ, Ortuño VM (2015) Exceptional invertebrate diversity in a scree slope in Eastern Spain. *Journal of Insect Conservation* 19: 713–728. <https://doi.org/10.1007/s10841-015-9794-1>
- Jones M (2022) Mapping the geography of underground ecosystems. ArcUser Spring. <https://www.esri.com/about/newsroom/arcuser/karst/>
- Juberthie C, Delay D, Bouillon M (1980) Extension du milieu souterrain en zone non calcaire: description d'un nouveau milieu et de son peuplement par les Coléoptères troglobies. *Mémoires de Biospéologie* 8: 77–93.
- Kampolis I, Triantafyllidis S, Skliros V, Kamperis E (2022) Quaternary evolutionary stages of Selinitsa Cave (SW Peloponnese, Greece) reveal sea-level changes based on 3D scanning, geomorphological, biological, and sedimentological indicators. *Quaternary* 5: 1–13. <https://doi.org/10.3390/quat5020024>
- Lecours V, Devillers R, Schneider DC, Lucieer VL, Brown CJ, Edinger EN (2015) Spatial scale and geographic context in benthic habitat mapping: review and future directions. *Marine Ecology Progress Series* 535: 259–284. <https://doi.org/10.3354/meps11378>
- López H, Oromí P (2010) A pitfall trap for sampling the mesovoid shallow substratum (MSS) fauna. *Speleobiology Notes* 2: 7–11.
- Mammola S, Giachino PM, Piano E, Jones A, Barberis M, Badino G, Isaia M (2016) Ecology and sampling techniques of an understudied subterranean habitat: the Milieu Souterrain Superficiel (MSS). *The Science of Nature* 103: 88. <https://doi.org/10.1007/s00114-016-1413-9>

- Mammola S, Cardoso P, Culver DC, Deharveng L, Ferreira RL, Fišer C, Galassi DMP, Griebler C, Halse S, Humphreys WF, Isaia M, Malard F, Martinez A, Moldovan OT, Niemiller ML, Pavlek M, Reboleira ASPS, Souza-Silva M, Teeling EC, Wynne JJ, Zagmajster M (2019) Scientists' Warning on the conservation of subterranean ecosystems. *BioScience* 69: 641–650. <https://doi.org/10.1093/biosci/biz064>
- Mammola S, Amorim IR, Bichuette ME, Borges PAV, Cheeptham N, Cooper SJB, Culver DC, Deharveng L, Eme D, Ferreira RL, Fišer C, Fišer Ž, Fong DW, Griebler C, Jeffery WR, Jugovic J, Kowalko JE, Lilley TM, Malard F, Manenti R, Martínez A, Meierhofer MB, Niemiller ML, Northup DE, Pellegrini TG, Pipan T, Protas M, Reboleira ASPS, Venarsky MP, Wynne JJ, Zagmajster M, Cardoso P (2020) Fundamental research questions in subterranean biology. *Biological Reviews* 95: 1855–1872. <https://doi.org/10.1111/brv.12642>
- Martel EA (1894) *Les abîmes: les eaux souterraines, les cavernes, les sources, la spéléologie*. Librairie Charles Delagrave, Paris, 646 pp.
- McDermid GJ, Franklin SE, LeDrew EF (2005) Remote sensing for large-area habitat mapping. *Progress in Physical Geography: Earth and Environment* 29: 449–474. <https://doi.org/10.1191/0309133305pp455ra>
- Meira-Neto JAA, Clemente A, Oliveira G, Nunes A, Correia O (2011) Post-fire and post-quarry rehabilitation successions in Mediterranean-like ecosystems: Implications for ecological restoration. *Ecological Engineering* 37(8): 1132–1139. <https://doi.org/10.1016/j.ecoleng.2011.02.008>
- Nitzu E, Popa I, Giurginca A (2011) Invertebrate fauna (Coleoptera, Collembola, Diplopoda, Isopoda) collected in the karst areas of the Aninei-Locvei Mountains. *Travaux de l'Institut de Spéologie "Émile Racovitza"* 50: 15–35.
- Nitzu E, Dorobăț ML, Popa I, Giurginca A, Baba Ș (2018) The influence of geological substrate on the faunal structure of the superficial subterranean habitats. *Carpathian Journal of Earth and Environmental Sciences* 13: 383–393. <https://doi.org/10.26471/cjees/2018/013/033>
- Nitzu E, Nae A, Băncilă R, Popa I, Giurginca A, Plăiașu R (2014) Scree habitats: ecological function, species conservation and spatial-temporal variation in the arthropod community. *Systematics and Biodiversity* 12: 65–75. <https://doi.org/10.1080/14772000.2013.878766>
- Ortuño VM, Gilgado JD, Jiménez-Valverde A, Sendra A, Pérez-Suárez G, Herrero-Borgoñón JJ (2013) The “alluvial mesovoid shallow substratum”, a new subterranean habitat. *PLoS ONE* 8: e76311. <https://doi.org/10.1371/journal.pone.0076311>
- Parque Natural da Arrábida (2000) Plano de ordenamento: 1ª Fase – Estudos de caracterização, 2–120.
- Pipan T, López H, Oromí P, Polak S, Culver DC (2010) Temperature variation and the presence of troglobionts in terrestrial shallow subterranean habitats. *Journal of Natural History* 45: 253–273. <https://doi.org/10.1080/00222933.2010.523797>
- Presas JAC (2012) *Modelação da suscetibilidade à rotura e propagação de desabamentos na Arrábida*. Tese de mestrado, Geografia – Geografia Física e Ordenamento do Território, Universidade de Lisboa, Instituto de Geografia e Ordenamento do Território, 132 pp. <http://hdl.handle.net/10451/9370>
- QGIS Development Team (2020) QGIS Geographic Information System. Open Source Geospatial Foundation Project. <http://qgis.osgeo.org>
- Ramalho ML (2015) Aspetos geológicos e morfológicos da Serra da Arrábida. XXIX Curso de Actualização de Professores em Geociências, 51–60.

- Reboleira AS, Borges P, Gonçalves F, Serrano A, Oromí P (2011) The subterranean fauna of a biodiversity hotspot region – Portugal: an overview and its conservation. *International Journal of Speleology* 40: 23–37. <https://doi.org/10.5038/1827-806X.40.1.4>
- Rendoš M, Mock A, Jászay T (2012) Spatial and temporal dynamics of invertebrates dwelling karstic mesovoid shallow substratum of Sivec National Nature Reserve (Slovakia), with emphasis on Coleoptera. *Biologia* 67: 1143–1151. <https://doi.org/10.2478/s11756-012-0113-y>
- Rendoš M, Čejka T, Šteffek J, Mock A (2014) Land snails from subterranean traps exposed in a forested scree slope (Western Carpathians, Slovakia). *Folia Malacologica* 22: 255–261. <https://doi.org/10.12657/folmal.022.022>
- Rohner PT, Bächli G, Pollini Paltrinieri L, Duelli P, Obrist MK, Jochmann R, Blanckenhorn WU (2015) Distribution, diversity gradients and Rapoport's elevational rule in the black scavenger flies of the Swiss Alps (Diptera: Sepsidae). *Insect Conservation and Diversity* 8(4): 367–376. <https://doi.org/10.1111/icad.12114>
- Rudy J, Rendoš M, L'uptáčík P, Mock A (2018) Terrestrial isopods associated with shallow underground of forested scree slopes in the Western Carpathians (Slovakia). *ZooKeys* 2018: 323–335. <https://doi.org/10.3897/zookeys.801.24113>
- Sharma R, Srivastava N (2022) Detection and classification of potential caves on the flank of Elysium Mons, Mars. *Research in Astronomy and Astrophysics* 22: 065008. <https://doi.org/10.1088/1674-4527/ac684f>
- Tabib W, Goel K, Yao J, Boirum C, Michael N (2022) Autonomous cave surveying with an aerial robot. *IEEE Transactions on Robotics* 38: 1016–1032. <https://doi.org/10.1109/TRO.2021.3104459>
- Tanalgo KC, Oliveira HFM, Hughes AC (2022) Mapping global conservation priorities and habitat vulnerabilities for cave-dwelling bats in a changing world. *Science of The Total Environment* 843: 156909. <https://doi.org/10.1016/j.scitotenv.2022.156909>
- Trimmis KP (2018) Paperless mapping and cave archaeology: A review on the application of DistoX survey method in archaeological cave sites. *Journal of Archaeological Science: Reports* 18: 399–407. <https://doi.org/10.1016/j.jasrep.2018.01.022>

Supplementary material I

Characterization of each of the locations found in situ as colluvial Mesovoid Shallow Substratum (MSS): latitude, longitude and estimated area (m²)

Authors: Rita P. Eusébio, Paulo E. Fonseca, Rui Rebelo, Maria da Luz Mathias, Ana Sofia P. S. Reboleira

Data type: table (Excel file)

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/subtbiol.45.96332.suppl1>

Supplementary material 2

Literature review data Mesovoid Shallow Substrate's faunal communities

Authors: Rita P. Eusébio, Paulo E. Fonseca, Rui Rebelo, Maria da Luz Mathias, Ana Sofia P. S. Reboleira

Data type: Excel file

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/subtbiol.45.96332.suppl2>

Supplementary material 3

Results of criteria met for each location pinpointed as potential colluvial Mesovoid Shallow Substratum (MSS)

Authors: Rita P. Eusébio, Paulo E. Fonseca, Rui Rebelo, Maria da Luz Mathias, Ana Sofia P. S. Reboleira

Data type: Excel file

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/subtbiol.45.96332.suppl3>

Supplementary material 4

Abundance of invertebrates collected in colluvial Mesovoid Shallow Substratum (MSS) at the Arrábida National Park

Authors: Rita P. Eusébio, Paulo E. Fonseca, Rui Rebelo, Maria da Luz Mathias, Ana Sofia P. S. Reboleira

Data type: Excel file

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/subtbiol.45.96332.suppl4>

Supplementary material 5

Total invertebrate abundance, collected in colluvial Mesovoid Shallow Substratum (MSS) at the Arrábida National Park

Authors: Rita P. Eusébio, Paulo E. Fonseca, Rui Rebelo, Maria da Luz Mathias, Ana Sofia P. S. Reboleira

Data type: figure (.tiff file)

Explanation note: **A.** Total abundance of arthropods and molluscs; **B.** Total abundance of Arthropoda classes; and **C.** Total abundance of Insecta orders.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/subtbiol.45.96332.suppl5>